

THE DISTINCTION BETWEEN OLD SECONDARY AND CLIMAX SPECIES IN TROPICAL CENTRAL AMERICAN LOWLAND FORESTS^{1, 2}

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(Received on March 10, 1970)

In tropical lowlands, botanists and foresters, and students of vegetation generally, are facing an ever-increasing problem of placing forest communities and their components in their proper successional sequence. It is "ever-increasing" because the area of secondary or simply disturbed forest is ever-expanding, due to shifting agriculture, openings for grazing, selective logging or highgrading, and such consequences of population expansion as new roads and other improvements in transportation. For collectors, there is often a real dilemma when it comes to qualifying the seral stage to which their specimens belong, and similar problems are often confronted by those working on their specimen notes.

Obviously, some guidelines are needed to distinguish successional stages and here, as in many other activities related to identification, it is possibly best to use a combination of characteristics to recognize seral stages, rather than using a single factor.

Thus, table 1 (Budowski 1965) summarizes data obtained from a series of plots of known age and relatively well-known past history in tropical lowland forests of Costa Rica and Panama, with plentiful rainfall (over 2,000 mm with mean annual temperatures between 22° and 26°C). It can be seen that the comparisons are based on relative rather than absolute values and provide some criteria for placing seral stages in their proper sequence. For the last 8 years this scheme has been tested in several forests of Costa Rica and Panama and some improvements to this scheme, using certain outstanding characteristics, can now be suggested. It has also become evident that some pitfalls have to be avoided.

1. A paper given at the Symposium on "Tropical Ecology and Evolution", at the International Botanical Congress Seattle, U.S.A., 1969.

2. Data for this paper were compiled while the author was Head of the Forestry Department, Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica.

It is true that, whether one uses this scheme or not, there should be little difficulty in differentiating between the *pioneer* and *early secondary* communities or their components, and the old secondary and of course climax communities. Species of *Cecropia*, *Ochroma*, *Trema*, certain *Jacaranda* and *Schyzolobium* are too well-known by most botanists and plant ecologists to warrant detailed studies to place the communities to which they belong into their proper sequence.

The *real challenge* and most of the difficulties appear, however, when it comes to *differentiating between old secondary and climax communities*. In this connection, one should not forget that it was only some 30 years ago that ecologically orientated botanists, such as Chevalier and Aubréville, demonstrated in tropical Africa that what have been called undisturbed, virgin or sometimes climax forests in this continent, were really old secondary forests and that really undisturbed patches were extremely scarce if present at all in most African countries. It is likely that a closer scrutiny of tropical American forests, even those enjoying high rainfall and not subject to burning, will reveal that a much larger area is actually secondary. An example can be found in eastern Panama, where historical records definitely show that extensive areas now covered with dense forests were once open agriculture and savanna-like landscapes, supporting some 450 years ago, a population variously estimated to be between 400,000 and over 1 million.

At this stage we may, for convenience, consider the climax stage as the end product of a successional sere when a relatively stable, although certainly not static, community has been reached, particularly as regards floristic composition, structure and physiognomy, all of which do not appreciably change over the age span of the dominants. While such a qualification is admittedly not very precise, it helps nevertheless to point out appropriate characteristic differences compared to the old secondary community, this being the seral stage preceding the climax. Here, the changes in floristic composition, structure and physiognomy over the age span of dominants are relatively evident, the classical difference being of course the dissimilar floristic composition of the regeneration in comparison with the species of the upper canopy, tending in due time to replace it.

In this passage from old secondary to climax, several aspects deserve some elaboration for diagnosis, permitting one to arrive at the desired distinction.

The largest part of the dominant trees of the old secondary communities is typically deciduous, even in areas of high rainfall. The trees, usually with wide crowns, may occasionally reach a considerable diameter and height. In fact they may sometimes constitute the largest trees over the whole region and reach a relatively old age.

These dominants may also be present in adjacent drier formations, notably in the deciduous forest, where they are smaller in size, have a slower growth rate and may actually be perfectly considered as climax species. A high concentration of these species may therefore be considered as a good indication of the secondary nature of these communities. It is no secret to foresters of

tropical America that many of the densest stands of mahogany, *Swietenia macrophylla*, are found on old and extensive clearings. The example is even more striking for "cuipo", *Cavanillesia palatanifolia*. This species has a patchy occurrence, closely linked to old clearings, and is very common in Eastern Panama and adjoining Colombian lowlands.

A second important characteristic of high diagnosis value refers to epiphytes. The general pattern here may be summarized as follows: epiphytes are of course common on trunks and branches of trees of old secondary communities, but there are changes in the course of succession towards climax, all tending towards increased diversity among species and particularly life forms. There is also an increase in specialization within the different canopies occupied by different epiphyte species. For instance, though an old secondary forest might support a large epiphytic growth, these belong only to relatively few species which can be found growing over a considerable vertical range. An adjacent older community would, on the other hand, display greater species diversity and more specialized occupancy of different levels within the vertical profile. A good example, easily distinguished by visual observations, is found among the bromeliads, commonly known as "tank epiphytes". In climax communities there are more variations in size, form and position than in old secondary stages, where few species may be abundantly represented throughout the vertical range. It would be interesting to have similar data on orchids, ferns, mosses, Araceae and other epiphytic groups.

A third reliable visual characteristic of high diagnosis value is the variation in vines. Although very abundant in early secondary stages, these display more specialization in the course of succession, particularly in the diameter size. Moreover, many of them are concentrated along certain trees or groups of trees. The largest diameters are of course found on older communities and the very large size, with diameters over 20 cm, are usually restricted to forests undisturbed over a long time period.

The preceding three examples may be used as criteria of relatively easy application by visual observation to separate older secondary communities from still older or climax conditions. However, as a safety device, they should not be used alone. Other characteristics should be used, notably:

- (a) the distinction of strata; this becomes increasingly difficult with age,
- (b) the growth rate of stem diameters; this also decreases with age,
- (c) regeneration patterns, already referred to but not easy to measure since they require careful recording over large areas with many samples,
- (d) ways of dissemination of seeds or fruits,
- (e) hardness of stem, increasing with age of communities, and
- (f) size of fruit and seed as dispersal agents.

TABLE 1. Characteristics of arboreal components of seral stages in tropical American humid forests

	Pioneer	Early secondary	Late secondary	Climax
Age of communities observed, years	1-3	5-15	20-50	more than 100
Height, meters	5-8	12-20	20-30, some reaching 50	30-45, some up to 60
Number of woody species	few, 1-5	few, 1-10	30-60	up to 100 or a little more
Floristic composition of dominants	Euphorbiaceae, <i>Cecropia</i> , <i>Ochroma</i> , <i>Trema</i>	<i>Ochroma</i> , <i>Cecropia</i> , <i>Trema</i> , <i>Heliocarpus</i> most frequent	mixture, many Meliaceae Bombacaceae, <i>Tilia</i> - ceae	mixture, except on edaphic association
Natural distribution of dominants	very wide	very wide	wide, includes drier regions	usually restricted, en- demics frequent
Number of strata	1, very dense	2, well differentiated	3, increasingly difficult to discern with age	4-5, difficult to discern
Upper canopy	homogeneous, dense	verticillate branching, thin horizontal crowns	heterogeneous, includes very wide crowns	many variable shapes of crowns
Lower stratum	dense, tangled	dense, large herbaceous species frequent	relatively scarce, includes tolerant species	scarce, with tolerant species
Growth	very fast	very fast	dominants fast, others slow	slow or very slow
Life span, dominants	very short, less than 10 years	short, 10-25 years	usually 40-100 years, some more	very long, 100-1000, some possibly more
Tolerance to shade, domi- nants	very intolerant	very intolerant	tolerant in juvenile stage, later intolerant	tolerant, except in adult stage
Regeneration of dominants	very scarce	practically absent	absent or abundant with large mortality in early years	fairly abundant
Dissemination of seeds of dominants	birds, bats, wind	winds, birds, bats	wind principally	gravity, mammals, rod- ents birds
Wood and stem, domi- nants	very light, small dia- meters	very light, diameters below 60 cm.	light to medium hard, some very large stems	hard and heavy, includes large stems
Size of seed, or fruits dispersed	small	small	small to medium	large
Viability of seeds	long, latent in soil	long, latent in soil	short to medium	short
Leaves of dominants	evergreen	evergreen	many deciduous	evergreen
Shrubs	many, but few species	relatively abundant but few species	few	few in number but many species
Epiphytes	absent	few	many in number, but few species	many species and life forms
Vines	abundant, herbaceous, but few species	abundant, herbaceous but few species	abundant, but few of them large	abundant, includes very large woody species
Grasses	abundant	abundant or scarce	scarce	scarce

When a community is analysed according to such a questionnaire, it will fall into a certain pattern, even if one or two factors do not quite correspond. The latter allowance is only to be expected when natural communities are influenced by natural disturbances (wind, floods, death and crash of an old tree or of groups of trees, etc.).

Now let us move to the pitfalls of such methodology.

An obvious example is that of early pioneers. Never should the presence alone of the pioneers be enough to qualify the community as one belonging to the early stages of succession. Even in clearly undisturbed forest areas, there will always be natural openings such as creeks or rivers or the hole produced by the fall of a big tree. These result in openings or edge effects which are sufficiently large to allow the spread and development of what Van Steenis has aptly called 'biological nomads' (Van Steenis 1958).

The problem again becomes much more complicated in older communities. The first consideration is the recognition of special soil factors. As a general rule, whenever such factors as flooding, waterlogging, impeded poor drainage, or very shallow soils prevail, the trend will be towards simplification and the successional pattern as described previously will be modified. In some cases the climax community may actually be simpler in floristic composition than the preceding secondary vegetation. This is certainly the case with the "cativo" stands, (*Prioria copaifera*), on alluvial elevated river banks which are only flooded occasionally, or the *Carapa* and *Virola* forests in more frequently inundated areas, where, in extreme cases, *Mora excelsa*, *Campnosperma panamensis*, *Pterocarpus officinalis* occur in practically pure association. In all these communities the strata can easily be distinguished.

Hurricanes or very strong winds, even if they occur on average only once every 30 years, may also affect succession. In Central America they affect extensive areas on exposed sites along the Pacific coast of Costa Rica and Panama and on the Atlantic coastal forests of Nicaragua, Honduras and northwards. Their actions may be such as to prevent the establishment of the typical climax. Likewise, even moderately strong gusts of wind will often induce the downfall of large trees growing on shallow soils, thereby causing too many holes and secondary patches to enable the easy classification of seral stage. In areas of very heavy rainfall, the root system may often be so shallow that succession will never be allowed to progress for long periods without disturbance, because of continuous uprooting of trees.

The disturbance caused by man often leads to confusion in the recognition of successional patterns. When fields are clearcut and planted for a few years, prior to abandonment, old secondary forests are still distinguishable, even 50–100 years after they have been established, from nearby climax communities because of the remnant of a sharp boundary. But in many clearings, it was customary and is still common in Central America, that some of the hard and heavy wooded trees which are clearcut climax species, such as *Coumarouna* or *Dypterix*) *panamensis* or some *Lecythidaceae* or *Sapotaceae*, will often be left standing because of their extreme hardness. Again a confusing picture results,

since some of the trees do not fall over or die in spite of being isolated. Fortunately for the student of successions, the varied epiphytic vegetation and many of the vines will not resist such exposure over a long period of time, and their absence becomes a good index of past history.

Finally, there is also the importance of the size of man-made clearings and the intensity of soil depletion. In areas which are strongly degraded, the succeeding seral stages tend to change only very slowly before they eventually show marked changes in physiognomy, structure and floristic composition. The result may be extremely patchy over large areas, because of different rates of succession, even if it all may have started at the same time.

In conclusion, on the basis of experience in Central America, the search for distinctive characteristics should allow recognition of successional patterns and their pitfalls. Let us hope that permanent study plots be established in selected areas that will remain as living testimonies of the present and products of the fascinating successional picture...before it is too late.

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